DIVISION S-3—SOIL BIOLOGY & BIOCHEMISTRY

Short-Term Competition for Ammonium and Nitrate in Tallgrass Prairie

Curtis J. Dell* and Charles W. Rice

ABSTRACT

The availability of N limits productivity in tallgrass prairie. Spring burning is common because it results in greater plant productivity despite reducing net N mineralization. To better explain how burning affects inorganic N availability in tallgrass prairie, the partitioning of ^{15}N among plant and soil pools was measured in June and August 1994. Approximately 2.5 μg N g^{-1} soil was injected as either NH_4 or NO_3 to a depth of 15 cm within cores in burned and unburned prairie. Cores were removed from the field 6 d after injection, and ^{15}N recovery in plant and soil N pools was determined. No more than 14% of the applied ^{15}N remained in inorganic form 6 d after application. The largest portion of the applied ^{15}N (35–80%) was recovered in the soil organic nitrogen pool (N_o). Burning significantly increased the immobilization of both NH_4 and NO_3 within N_o, and microbial biomass accounted for ≥50% of the ^{15}N recovered in N_o. Accumulation of ^{15}N in plants accounted for ≤35% of the applied ^{15}N with a majority recovered from roots. Burning had little effect on ^{15}N recovery in plants; however, ^{15}N accumulations in roots were significantly greater when NO_3 was used. Results indicate that immobilization within soil organic matter (SOM) controls the availability of both NH_4 and NO_3 to plants. Increased immobilization in soils with burning probably results largely from increased microbial N demand resulting from greater litter inputs with wider C to N ratios. Further research is needed to determine if abiotic mechanisms for N immobilization also significantly influence N availability in prairie soils.

With the exception of water deficits in some years, the availability of N is generally considered to be the largest limitation to plant growth in tallgrass prairie (Owensby and Smith, 1979). However, the response to fertilizer additions is generally much greater in years when prairie is burned (Owensby and Smith, 1979; Seastedt et al., 1991). Seastedt et al. (1991) observed a 9% increase in foliage production with fertilization (10 g N m^{-2}) in prairie unburned for 15 yr. The same rate of fertilizer resulted in a 45% increase when applied in the year of a springtime burn. The authors concluded that the microclimatic limitations to plant growth created by the accumulation of surface litter can be greater than N limitations. The removal of surface litter by fire reduces shading and insulation of the soil surface resulting in warmer early season soil temperatures, earlier regrowth, and greater plant biomass production (particularly warm-season grasses) (Knapp and Seastedt, 1986). As plant biomass production increases in response to burning, quantities of available soil N may not be sufficient to meet plant demand.

Although the total mass of N in the Konza Prairie in Kansas is relatively large (approximately 650 g N m^{-2} to a depth of 25 cm), the pool of plant-available NH_4 and NO_3 generally represents less than 0.1% of the total N in the system. Inputs of N through N_2 fixation and precipitation are small (1–2 g m^{-2}), and can be offset by the loss of 1 to 4 g N m^{-2} to fire (Blair et al., 1998). Therefore, mineralization of organic N must supply the majority of N needed by both plant and soil microbial populations. Annual burning has also been shown to decrease net N mineralization rates, and, therefore, quantities of plant-available inorganic N compared with unburned prairie (Ojima et al., 1994; Blair, 1997; Turner et al., 1997; Johnson and Matchett, 2001). Measurements of gross N transformation rates in tallgrass prairie soils indicate that potential daily consumption of both NH_4 and NO_3 exceeds daily production (Williams et al., 2001; Dell, 1998; Garcia, 1992). Because burning appears to have little effect on gross mineralization rates (Dell, 1998) or quantities of potentially mineralized N (Dell, 1998; Garcia, 1992), reductions in net mineralization with burning probably result from greater immobilization rather than lower production rates. Increased microbial immobilization in soil following burning is probably a response to larger organic matter inputs with wider C to N ratio (Ojima et al., 1994).

Because microbial N demand in tallgrass prairie is high and the pool of inorganic soil N is low, the ability of plants to compete with microbes for that N could greatly affect their productivity. Jackson et al. (1989) investigated the competition for both NH_4 and NO_3 in an annual grassland in California. They reported that daily uptake of NH_4 by plants and microbes was nearly equal to the extractable pool and that NO_3 appeared to be consumed as quickly as it was produced. More of the applied ^{15}N was recovered from soil microbes than from either plants or the soil inorganic N pool, both early and late in the growing season. DeLuca and Keeney (1995) traced the fate of ^{15}N-labeled NO_3 in tallgrass prairie soil. They found that 24 h after application the largest portion of the tracer was recovered from the soil organic fraction, but after 72 h a larger portion was recovered in the plants.

The competition between plants and soil microbes for both NH_4 and NO_3 has not been reported for tallgrass prairie. Microbial assimilation of NO_3 is generally not

C.J. Dell, USDA-ARS-PSWMRU, University Park, PA 16802; C.W. Rice, Department of Agronomy, 2004 Throckmorton Hall, Kansas State University, Manhattan, KS 66506. Contribution no. 01-376-J of the Kansas Agricultural Experiment Station. Received 8 Dec. 2003. *Corresponding author (curtis.dell@ars.usda.gov).

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677 S. Segoe Rd., Madison, WI 53711 USA

Abbreviations: N_i, soil inorganic nitrogen pool; N_o, soil organic nitrogen pool; SOM, soil organic matter.

expected in the presence of NH_4, because enzymes active in the microbial uptake of NO_3 are inhibited by as little as 0.1 μg NH_4–N g^{-1} (Rice and Tiedje, 1989). This assumption could lead to the prediction that soil microbes will not compete strongly with plants for available NO_3. However, substantial microbial assimilation of NO_3 has been reported in soils with detectable concentrations of NH_4 (Davidson et al., 1990; Jackson et al., 1989). In these cases, NO_3 appears to have been assimilated within microsites where NH_4 was depleted.

A better understanding of competition for both NH_4 and NO_3 among plant and soil pools is needed to explain how the uptake of N by plants is affected by annual burning in tallgrass prairie. To address the fate of newly available inorganic N, the partitioning of small additions of ^{15}N-labeled NH_4 and NO_3 was determined 6 d after injection into soils of annually burned and unburned tallgrass prairie. The 6-d incubation period provided sufficient time for plant uptake but was short enough to minimize remineralization of immobilized ^{15}N. The study was repeated within the growing season to compare N partitioning at two distinctly different stages of plant growth.

MATERIALS AND METHODS

The study was conducted at the Konza Prairie Research Natural Area near Manhattan, Kansas. The plant community at the site is dominated by the C_4 grasses big bluestem (*Andropogon gerardii* Vitman), switchgrass (*Panicum virgatum* L.), and Indian grass [*Sorghastrum nutans* (L.) Nash]. A wide variety of cool-season grasses and forbs are also found with the greatest number observed in unburned prairie. In 1986, a randomized block experiment with four replicates was established to study the effect of annual burning and fertilization on belowground processes in the tallgrass prairie. The current experiment was conducted within the unfertilized control plots of each burned and unburned block. Annual burning occurs in late April or early May. The soil at the site is mapped as an Irwin silty clay loam (fine, mixed, mesic, Pachic Argiustolls). Total C and N contents of the soil are approximately 3.1 and 0.28 g kg^{-1}, respectively, and have not changed significantly with annual burning (Dell, 1998). The soil is somewhat acid with pH values ranging from 5.6 to 6.1 with no differences between burned and unburned treatments (Ajwa et al., 1999).

In May and again in July of 1994, two 25-cm-diameter by 25-cm-long PVC cores were inserted to a depth of approximately 20 cm into each of four replicates of the annually burned and unburned prairie treatments. Four weeks later, 14 mg of ^{15}N (approximately 2.5 μg N g^{-1} soil or 0.30 g N m^{-2}) was injected into each core to a depth of 15 cm using multiple injections with a spinal needle (17 gauge, 15 cm long; Popper and Sons, Hyde Park, NY). Solution was injected into the 0- to 5- and 5- to 15-cm layers separately with each layer receiving 13 injections. Needles were inserted to a depth of either 5 or 15 cm with a solid insert. The insert was removed and solutions were injected as the needle was raised out of the soil. One core in each plot received $(^{15}NH_4)_2SO_4$ (98% enrichment), while the other received $K^{15}NO_3$ (96% enrichment).

The cores were removed from the field 6 d after ^{15}N application. In the laboratory, the foliage was cut at the soil surface, the soil removed from the core, and all soil greater than 15 cm from the surface separated from the top 15 cm of soil. Large roots and rhizomes were removed. The soil was then passed through a 6-mm sieve and mixed, and a subsample was removed for analysis. Remaining soil was washed to recover small roots and root fragments. The soil was placed in a plastic container, flooded, and shaken repeatedly, with the wash water passed through a 0.5-mm sieve after each shaking. Soil samples were stored at 4°C until analysis. The plant material was dried for 3 d at 60°C and ground to pass through a 1-mm screen. The estimated mass of small roots in the subsamples was added to the mass of recovered roots, assuming the concentration of roots in the subsample was the same as in the washed soil. No roots were removed from soil greater than 15 cm from the surface, but the soil was analyzed for total ^{15}N. Soil and plant material was also obtained from outside the cores to provide natural abundance ^{15}N concentrations.

Soil samples (20 g) were extracted in 100 mL of 1 *M* KCl three times by shaking for 1 h at 300 rpm. After shaking, samples were centrifuged for 10 min at 15 000 × *g*. The first extract was saved for analysis of ^{15}N as NH_4 and NO_3 (inorganic nitrogen, N_i). After the third extraction, the soil was freeze-dried and analyzed to determine ^{15}N in the soil organic nitrogen (N_o) (microbial biomass plus nonbiomass organic matter components) (Williams et al., 2001). Total NH_4 and NO_3 concentrations of KCl extracts were determine colorimetrically by autoanalyzer (Alpkem Corp., Clackamas, OR) after which extracts were prepared for isotope analysis by the diffusion method (Brooks et al., 1989). Forty milliliters of extract were transferred to 120-mL specimen cups and approximately 0.4 g of MgO and 0.5 g Devarda's metal was added to each. Small filter disks (Whatman [Maidstone, UK] GF/D) were acidified with 2.5 *M* $KHSO_4$ (pH 3.5) and suspended over the extracts on bent wires. Cups were sealed, gently swirled, and then left undisturbed for 6 d. After 6 d, filter disks were dried and transferred to tin capsules for analysis. If 40 mL of extract contained less than 50 μg N, 40 μg of N was added to the cup before diffusion.

To determine mass of ^{15}N in microbial biomass, 25-g soil samples were fumigated with chloroform for 48 h and then immediately extracted with 0.5 *M* K_2SO_4 (Brookes et al., 1985). An additional 25 g of soil was extracted without fumigation. Persulfate digestion (Cabrera and Beare, 1993) was used to prepare K_2SO_4 extracts before analysis. Three milliliters of extract was combined with 4.2 mL persulfate solution (low-N $K_2S_2O_8$, 50 g L^{-1}; H_3BO_3, 30 g L^{-1}; and 3.5 *M* NaOH, 100 mL L^{-1}) and autoclaved for 30 min at 120°C. The determination of total NH_4 and NO_3 concentrations and diffusion in preparation for isotope analysis followed the procedure described for KCl extracts. The mass of ^{15}N contained in microbial biomass (MBN) was calculated by dividing the difference in ^{15}N mass between fumigated and unfumigated soils divided by 0.45 to correct for extraction efficiency (Jenkinson et al., 2004)

Total N concentrations and isotope ratios of plant material and soils, and isotope ratios of diffused extracts were measured using an Europa Scientific ANCA-SL isotope-ratio mass spectrometer (PDZ Europa, Northwich, UK).

Separate analyses of variance (ANOVAs) were calculated to assess the effects of burning and form of applied N on ^{15}N recovery from each N pool using SAS PROC GLM (SAS Institute, 2001). Results from June and August were analyzed individually. Data met normality criteria and were not transformed. Differences among means for combinations of burning and N-form treatments were analyzed using the LSMEANS option of PROC GLM. Because of naturally high spatial variability in plant distribution in the native prairie, differences were considered significant at $p \leq 0.10$ unless otherwise stated.

RESULTS

June

Recovery of applied ^{15}N was nearly complete and the immobilization of applied ^{15}N was rapid with <15% of

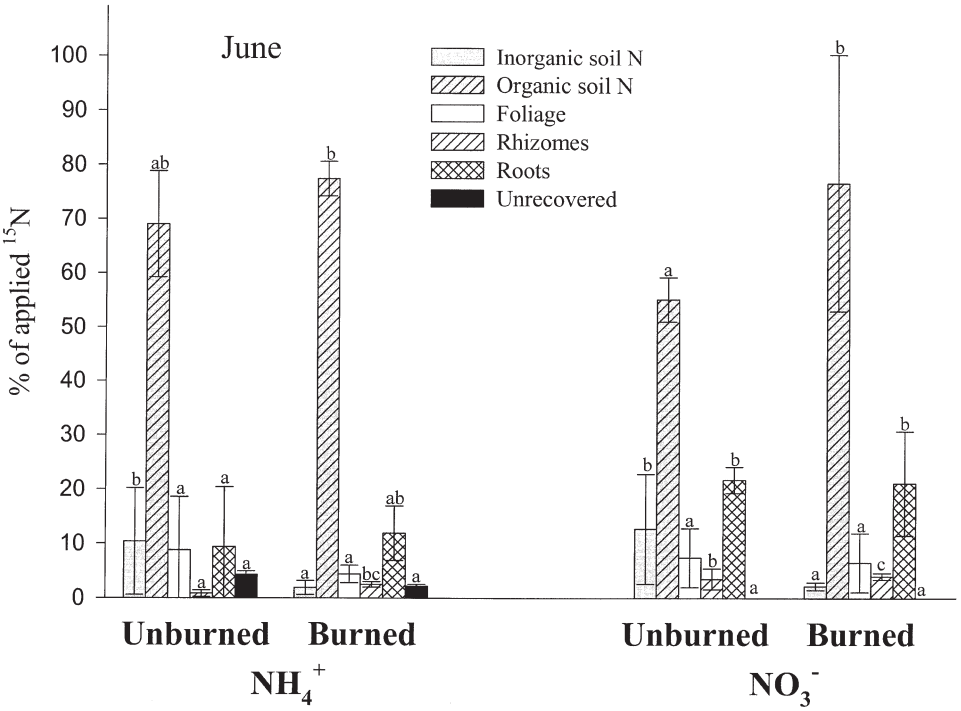

Fig. 1. Mean distribution of ^{15}N among soil and plant pools 6 d after application as either NH_4 or NO_3 at the Konza Prairie, Kansas, in June 1994. Error bars are the standard deviation of four replicates. Bars for the same N pool accompanied by the same letter do not differ significantly among combinations of burning and N source treatments ($p \leq 0.10$).

the applied N remaining as NH_4 or NO_3 after 6 d (Fig. 1). Significantly less ^{15}N remained as N_i in burned prairie compared with unburned when applied as either NH_4 or NO_3. The largest portion of the applied ^{15}N (55–75%) was recovered from N_o (Fig. 1), which contains >95% of the total N in the sampling zone (Table 1). Analysis of variance indicated that burning significantly affected both the uptake of inorganic ^{15}N and the accumulation in N_o but that the form in which N was applied did not affect mass of ^{15}N in soil pools. Microbial biomass N accounted for approximately half of the ^{15}N recovered from the soil organic fraction regardless of burning or form in which N was applied; however, variability among replicates was high and no differences among treatment combinations were determined (data not shown).

Accumulation of ^{15}N in the three plant components was consistently less than in N_o and accounted for approximately 20 to 35% of the applied ^{15}N (Fig. 1). Regardless of burning or applied form of N, the majority of ^{15}N accumulated in plants was found in the roots (Fig. 1), which contained >75% of the total mass of N in the plant (Table 1). Analysis of variance indicated no significant effect of burning on recovery of ^{15}N in foliage or roots (Table 2). Tracer recovery in rhizomes was significantly increased by burning; however, ^{15}N accumulation in rhizomes was low regardless of treatment combination. Mean biomass of the each of the three plant components was larger in burned prairie compared with unburned, but the difference was significant only for roots (Table 3). Accumulations of ^{15}N in roots and rhizomes were generally greater when the tracer was applied as NO_3 (Fig. 1) with the effect of applied N form significant in ANOVA for both pools (Table 2).

August

The overall recovery of applied ^{15}N was lower (65–75%) in August than June (98%), but the distribution of recovered ^{15}N was similar (Fig. 2). The quantities of ^{15}N remaining as N_i 6 d after application were similar to those observed in June (≤10% of applied ^{15}N). However, unlike June, burning did not affect the quantity

Table 1. Total N mass in each pool to a depth of 15 cm at the Konza Prairie, Kansas, in June and August 1994.†

	June		August	
N pool	Unburned	Burned	Unburned	Burned
	g N m^{-2}			
Foliage	0.46a (0.41)	0.85a (0.39)	0.72a (0.66)	0.70a (0.20)
Rhizomes	0.50a (0.32)	1.06b (0.78)	0.75a (0.40)	0.94a (0.22)
Roots	4.77a (1.67)	5.87a (2.04)	5.56a (1.46)	4.53a (1.93)
Soil NH_4	0.53b (0.18)	0.19a (0.06)	0.33b (0.04)	0.13a (0.01)
Soil NO_3	0.71b (0.44)	0.10a (0.06)	0.17a (0.09)	0.02a (0.03)
Soil organic N	191.7a (14.05)	202.27a (53.27)	156.8a (54.74)	162.07a (56.01)

† Values in parentheses are standard deviations of eight replicates per burning treatment and sampling date. Means for the same N pool and sampling date accompanied by the same letter do not differ between burning treatments at $p \leq 0.10$.

Table 2. Analysis of variance (ANOVA) of the main effects of annual burning and applied N form (NH_4 or NO_3) on the recovery of ^{15}N in plant and soil N pools 6 d after application at the Konza Prairie, Kansas, in June and August 1994 (n = 4 per treatment and sampling date).

	June				August			
	Burning		N form		Burning		N form	
N pool	*F* value	$p > F$	*F* value	$p > F$	*F* value	$p > F$	*F* value	$p > F$
Foliage	0.59	0.4627	0.02	0.8843	6.61	0.0331	7.44	0.0260
Rhizomes	3.37	0.0998	14.16	0.0045	0.01	0.9262	0.01	0.9144
Roots	0.10	0.7636	6.22	0.0373	2.61	0.1451	7.55	0.0252
Soil inorganic N	10.44	0.0103	0.21	0.6602	0.01	0.9343	0.78	0.3997
Soil organic N†	6.18	0.0346	1.54	0.2458	14.60	0.0041	1.63	0.2342

† Including microbial biomass N.

of ^{15}N remaining in the inorganic form (Table 2). As in June, the largest portion of applied ^{15}N was recovered from the soil organic fraction. Accumulations of ^{15}N in N_o of the unburned treatment where NO_3 was the N source were lower than all other treatments, and burning resulted in greater accumulations in N_o when tracer was applied as NH_4 (Fig. 2). The mass of ^{15}N recovered from microbial biomass in each treatment combination was similar to that recovered in June. Because overall ^{15}N recovery was lower in August, microbial biomass accounted for as much as 80% of N_o. However, high variability among replicates was again observed and treatment combinations were not different.

Quantities of ^{15}N recovered in plant components and the treatment effects on plant N uptake were similar in June and August (Fig. 2). Analysis of variance indicated that foliage ^{15}N accumulations were significantly affected by both burning and application of ^{15}N as NO_3 (Table 2). Although total recovery of applied ^{15}N was substantially lower in August than June, the mass of ^{15}N recovered from roots was similar for the two sampling dates. As in June, ANOVA showed that ^{15}N accumulation in roots was not affected by burning but that it was significantly greater when N was applied as NO_3 (Table 2 and Fig. 2).

Nitrogen-15 concentrations of the soil immediately below the application zone were as much as 21% greater than natural abundance (data not shown), indicating downward movement of applied N. Because soil cores had an open bottom, the total mass of ^{15}N below the application depth could not be quantified.

DISCUSSION

Greater than 85% of ^{15}N recovered 6 d after application was immobilized within soil organic matter (SOM) or plants regardless of burning or the form in which N was applied, supporting the view that N demand is high in the tallgrass prairie ecosystem (Owensby and Smith, 1979; Seastedt et al., 1991). Soil organic matter was the by far the largest sink for applied ^{15}N, indicating that microbial uptake and, possibly, abiotic mechanisms for the direct incorporation of inorganic N into SOM (Barrett et al., 2002; Davidson et al., 1991; Johnson et al., 2000) can limit the availability of both NH_4 and NO_3 to plants. Immobilization of both NH_4 and NO_3 within SOM increased with burning. Wider C to N ratios of organic matter inputs in burned prairie occur when both above- and belowground plant biomass production increases without an increase in N inputs (Ojima et al., 1994). Increased root biomass production in burned prairie generally offsets or exceeds quantities of aboveground biomass lost to burning (Rice et al., 1998). Therefore, greater immobilization of inorganic N within soil of burned prairie is probably largely due to increased microbial N demand in response to greater inputs of lower-quality litter. Hodge et al. (2000) showed that soil C to N ratio greatly affected the ability of perennial ryegrass to assimilate N. They observed that 45 to 54% of the applied ^{15}N was assimilated by plants in soils with C to N ratios of <4:1, but only 11% was recovered in plants when the soil C to N ratio was 21:1. Although the current study represents data from only one location, our finding supports previous observations that soil microorganisms control plant N uptake in N-limited ecosystems (Jackson et al., 1989; Kaye and Hart, 1997; Norton and Firestone, 1996; Williams et al., 2001).

Plant N uptake was consistently less than immobilization within SOM. Nitrate uptake by roots decreased in burned prairie indicating that greater immobilization within SOM further limited NO_3 availability to plants. It could be argued that the N demand of the plant community was simply much lower than that of microbial community and that the plant N demand was satisfied. However, fertilization experiments have shown plant responses to much larger additions of N than used in this experiment and that the response was greater in burned prairie (Owensby and Smith, 1979; Seastedt et al., 1991; Garcia, 1992). Therefore, it is assumed that plant N demand is not met in unfertilized prairie and plants are actively competing for the limited quantities of available N.

The incubation period used in this study limited our ability to determine the partitioning of immobilized ^{15}N within SOM pools. Using an extraction efficiency cor-

Table 3. Mass of plant components in June and August 1994 as affected by annual burning at the Konza Prairie, Kansas.†

	June		August	
	Unburned	Burned	Unburned	Burned
	g biomass m^{-2}			
Foliage	24a (19)	62a (35)	67a (57)	99a (41)
Rhizomes	75a (55)	184a (121)	115a (66)	188a (60)
Roots	475a (251)	726b (253)	666a (167)	727a (248)

† Values in parentheses are standard deviations of four replicates. Means for the same N pool and sampling date accompanied by the same letter do not differ between burning treatments at $p \leq 0.10$.

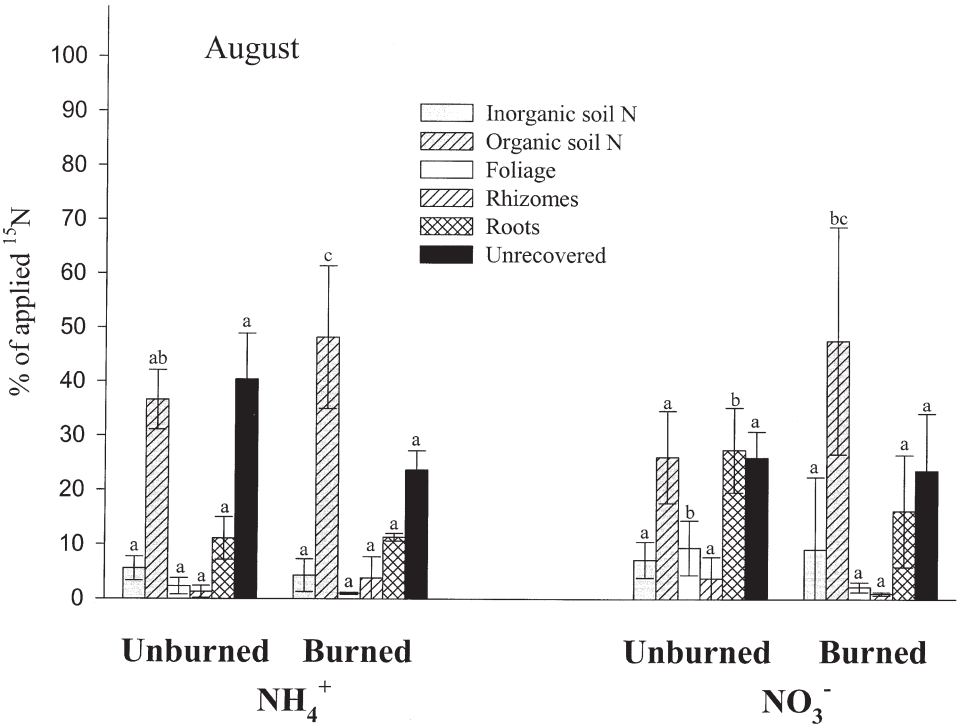

Fig. 2. Mean distribution of ^{15}N among soil and plant pools 6 d after application as either NH_4 or NO_3 at the Konza Prairie, Kansas, in August 1994. Error bars are the standard deviation of four replicates. Bars for the same N pool accompanied by the same letter do not differ significantly among combinations of burning and N source treatments ($p \leq 0.10$).

rection of 0.45 (Jenkinson et al., 2004), microbial biomass accounted for one-half to two-thirds of the ^{15}N recovered in the SOM. However, the mechanisms for the immobilization of the remaining ^{15}N recovered from SOM were not directly determined. A large portion of the nonbiomass ^{15}N in SOM is likely to have been processed through the microbial population, because the 6-d incubation period allowed sufficient time for cell turnover. Additionally, abiotic processes may have been responsible a portion of immobilization. Barrett et al. (2002) observed that abiotic processes accounted for 10 to 40% of the immobilization of inorganic N during laboratory incubations of 10 soils from grassland sites in the Great Plains. Currently, it is not clear whether prairie burning has the potential to influence abiotic interactions of NH_4 or NO_3 with SOM. Changes in plant community structure in response to burning may change the chemical composition of SOM and could alter chemical reactions with inorganic N. Moreover, interactions between inorganic N and charcoal and ash in burned prairie merit further research.

Difficulty in exactly quantifying microbial biomass N also limits our understanding of partitioning of immobilized N within SOM pools. Although chloroform fumigation and extraction with K_2SO_4 (Brookes et al., 1985) are commonly accepted as an effective way to liberate microbial biomass N for quantification, several factors have been suggested to correct for extraction efficiency (Brookes et al., 1985; Davidson et al., 1989; Jenkinson et al., 2004; Shen et al., 1984). Because determination of extraction efficiency was beyond our capabilities, we used the correction factor recommended by Jenkinson et al. (2004). However, pH and other soil chemical properties, or clay mineralogy, could potentially affect the extraction of N from a specific soil.

A lesser preference for NO_3 than NH_4 by soil microbes would have helped to explain how plants sustain productivity in the N-limited prairie. However, the incorporation of ^{15}N into SOM or microbial biomass was similar regardless of the form in which the N was applied. Because the presence of NH_4 generally inhibits microbial NO_3 assimilation (Rice and Tiedje, 1989) and some NH_4 was detected in the bulk soil from each replicate, depletion of NH_4 at microsites within the soil aggregates is likely to have resulted in microbial assimilation of NO_3.

When $^{15}NO_3$ was applied to the soil surface of tallgrass prairie at a rate that was approximately four times greater than in the current study, DeLuca and Keeney (1995) found that a greater portion of the applied N was recovered from roots than was immobilized in soil 72 h after application. A comparison of their study with ours is an indication that the addition of sufficient N to fulfill microbial demand and/or abiotic immobilization potential is needed before plant N assimilation exceeds immobilization in soil.

Although seasonal patterns cannot be determined from our observations at only two points in the growing season, similar distribution of recovered ^{15}N between plants and soil in June and August suggests that competition may limit N availability to plants throughout the growing season. Nitrogen content of aboveground plant biomass of some prairie grasses has been shown to decrease after midsummer (Old, 1969; Rains et al., 1975; Risser and Parton, 1982), leading to the expectation that

plant N requirements might have been lower in August than June. However, Risser and Parton (1982) and Old (1969) found no consistent seasonal trends in root N content. Owensby et al. (1977) showed that belowground N reserves in big bluestem declined throughout the middle of the growing season but increased from August through November. Decreasing N content of the aboveground portions of the grasses in the second half of the growing season may not signal decreasing N demand, but simply a change in the pattern of N allocation within the plant.

Despite greater N immobilization in soil with burning, prairie burned annually in the spring is consistently more productive than unburned prairie (Knapp et al., 1998; Owensby and Anderson, 1967; Rains et al., 1975). Burning generally increases the dominance of warm-season grasses, which have greater N use efficiency than most cool-season grasses and forbs (Owensby and Anderson, 1967). Therefore, sustained increases in plant productivity in burned prairie, despite lower N availability, may largely be possible because of N conservation within the grasses. Removal of N from senescing foliage and storage in roots and rhizomes during winter minimizes the quantity of N that can be lost when aboveground litter is burned (Ojima et al., 1994). Two warm-season grasses, big bluestem and Indian grass, receive approximately 18% of their annual N requirement from internal reserves (McKendrick et al., 1975). Clark (1977) traced internal cycling of N in shortgrass prairie dominated by blue grama [*Bouteloua gracilis* (Kunth) Lag. ex Griffiths, nom. illeg.] and found that as much as one-third of the N contained in the shoots was translocated to belowground storage organs and was available for use the following growing season. A long-term ^{15}N study at the Konza Prairie (Dell et al., 2005), conducted in conjunction with the current study, indicated that quantities of ^{15}N recovered from plants one and two growing seasons after application as NH_4 were similar to quantities recovered 6 d after application. Clark (1977) observed that levels of immobilized ^{15}N in blue grama remained nearly constant up to 5 yr.

Although immobilization within SOM limits the availability of inorganic N to plants, the continued retention of N in SOM provides a pool of potentially mineralized N, which results in a small, but constant, supply of plant-available N. Williams et al. (2001) reported that 75 to 85% ^{15}N immobilized in tallgrass prairie soils was mineralized within approximately 300 d following application. Gross mineralization measurements in tallgrass prairie soil (Dell, 1998; Williams et al., 2001) indicated that daily production of inorganic N was comparable with, or somewhat larger than, the size of the standing pools. Clark (1977) hypothesized that tight recycling of N within the rhizosphere plays an important role in maintaining N levels within short-grass prairie plants. He proposed that a large portion of N leaving roots in exudates is taken up by microbes and subsequently re-immobilized by the roots as microbial cells turn over.

Lower total ^{15}N recovery in August than in June may have been caused by the drainage of ^{15}N below the sampling zone. Because the cores had open bottoms, quantification of the mass of ^{15}N below the application zone was not possible. The ^{15}N enrichment of the soil immediately below the sampling zone, however, was as much as 20% greater than before N application (data not shown). The soil water content was only 14 g 100 g^{-1} soil at the time of application in August. Even though no measurable precipitation occurred during the incubation period, it is likely that a portion of the injected solutions flowed below the injection layer through unsaturated macropores. Substantial denitrification losses would not be expected given the soil water content in August.

CONCLUSIONS

The demand for inorganic N in tallgrass prairie soils is high and immobilization within SOM appears to control quantities of both NH_4 and NO_3 that are available to plants. Burning resulted in greater incorporation of ^{15}N into SOM when applied as either NH_4 or NO_3. This increased immobilization in soil was probably due largely to greater microbial N demand in response to larger total C inputs with a wider C to N ratio. Because one-half or more of the applied ^{15}N was accounted for in the microbial biomass, microbial assimilation was probably responsible for the incorporation of most of the N into SOM. But, further research is needed determine if abiotic mechanisms contribute significantly to the immobilization of NH_4 and NO_3 in these soils. Although total ^{15}N recovery was lower in August than June, the distribution of recovered ^{15}N among plant and soil N pools was similar in the two months, suggesting that the availability of inorganic N to plants is probably limited throughout the growing season.

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